Electrophysiological Correlates of Similarity-based Interference during Detection of Visual Forms

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Abstract

Illusory figure completion demonstrates the ability of the visual system to integrate information across gaps. Mechanisms that underlie figural emergence support the interpolation of contours and the filling-in of form information [Grossberg, S., & Mingolla, E. Neural dynamics of form perception: Boundary completion, illusory figures and neon colour spreading. Psychological Review, 92, 173–211, 1985]. Although both processes contribute to figure formation, visual search for an illusory target configuration has been shown to be susceptible to interfering form, but not contour, information [Conci, M., Müller, H. J., & Elliott, M. A. The contrasting impact of global and local object attributes on Kanizsa figure detection. Submitted]. Here, the physiological basis of form interference was investigated by recording event-related potentials elicited from contour- and surface-based distracter interactions with detection of a target Kanizsa figure. The results replicated the finding of form interference and revealed selection of the target and successful suppression of the irrelevant distracter to be reflected by amplitude differences in the N2pc component (240–340 msec). In conclusion, the observed component variations reflect processes of target selection on the basis of integrated form information resulting from figural completion processes.

INTRODUCTION

Illusory figures demonstrate the ability of the visual system to integrate missing information across gaps. Natural scenes typically contain multiple overlapping objects, providing only suboptimal viewing conditions. Within such environments, one plausible biological function for figural completion processes refers to the registration of objects that would otherwise be camouflaged. This “anti-camouflage” mechanism (Ramachandran, 1987) provides the phenomenal emergence of figural information. For example, in Figure 1A (T), a square is induced and perceived as occluding neighboring parts of the four “circular” inducer elements. Phenomenally, the emergence of shape information is experienced in terms of a bright central region delineated by sharp boundaries, in the absence of a corresponding physical correlate (Kanizsa, 1955).

Related approaches designed to isolate the neural mechanisms underlying figural completion processes have identified various sources along the ventral stream. Results from physiological recordings indicate that cells in V1 and V2 code illusory contours comparable to real contours (Lee & Nguyen, 2001; Peterhans & von der Heydt, 1991; von der Heydt, Peterhans, & Baumgartner, 1984). Whereas activations specific to illusory contours have also been found in striate and extrastriate visual areas in humans (Ritzl et al., 2003; Murray, Wylie, et al., 2002; Ffytche & Zeki, 1996), a major source of processing has also been located in the lateral occipital complex (LOC) and fusiform gyrus (Halgren, Mendola, Chong, & Dale, 2003; Stanley & Rubin, 2003; Hirsch et al., 1995). Consistent with extrastriate sources of illusory figure perception, human electrophysiological correlates have typically been identified in the time range of the N1 component peaking at ~80–150 msec after stimulus onset at occipitoparietal sources (Murray, Foxe, Javitt, & Foxe, 2004; Murray, Wylie, et al., 2002; Pegna, Khateb, Murray, Landis, & Michel, 2002). Thus, activity elicited by illusory figures appears to be represented in various regions specialized in object processing. Early V1 and V2 activations within this pattern may reflect the interpolation of contours, whereas LOC and fusiform gyrus activity may be associated with the filling-in of surface information (Stanley & Rubin, 2003; see also Grossberg & Mingolla, 1985, for a related computational model).

To relate outcomes from physiological studies to behavioral measures, psychophysical investigations attempted to uncover the processes underlying object completion by employing visual search techniques. Experiments typically require observers to search for a target among distracter items, with reaction time (RT) measures, in particular, the search rate (i.e., the slope of the function relating search RT to the number of items in the display), allowing efficient search to be
distinguished from inefficient search (Treisman & Gelade, 1980). For example, Davis and Driver (1994) found that search for a Kanizsa square could be performed independently of the number of distracter configurations presented concurrently with the target (see Figure 1A-I for examples of target [T] and distracter [D] stimuli). This finding of efficient, spatially “parallel” search was taken to reflect early V2 activations in response to virtual contours (von der Heydt et al., 1984). However, closer examination of this finding has called into question the specific impact of illusory figures on search performance (Gurnsey, Poirier, & Gascon, 1996; but see also Gurnsey, Humphrey, & Kapitan, 1992). Consequently, follow-up experiments were carried out to identify how shape attributes are coded for search.

One study (Conci, Müller, & Elliott, submitted) examined the extent to which variations in contour and surface properties of distracters modify the efficiency of target Kanizsa figure detection. In the main experiment, eight observers (two men; mean age 27.1 years) performed a visual search task in which a target Kanizsa figure had to be detected among distracters that presented either only contour information (see Figure 1A for examples of target [T] and distracter [D] stimuli). This finding of efficient, spatially “parallel” search was taken to reflect early V2 activations in response to virtual contours (von der Heydt et al., 1984). However, closer examination of this finding has called into question the specific impact of illusory figures on search performance (Gurnsey, Poirier, & Gascon, 1996; but see also Gurnsey, Humphrey, & Kapitan, 1992). Consequently, follow-up experiments were carried out to identify how shape attributes are coded for search.

The precise stimulus parameters, experimental design, and procedure were essentially the same as those used in the present study (see Methods) except that display size was varied, with up to eight configurations presented in circular arrangement around central fixation.

Figure 1A and B also lists the mean target-present search RT slopes (in milliseconds per item) for each possible target–distracter pairing. Repeated measures analyses of variance (ANOVA) of the RT slopes with the factor number of collinear distracter contours (0, 1, 2; see Figure 1A and B), performed separately for the border and form distracter conditions, revealed a significant, pronounced slowing of search rates with distracters that presented surface variations [from 12 (baseline) to 80 msec/item; \(F(2,14) = 68.19, p < .001\); see Figure 1B], but not with distracters that presented contours in isolation [from 11 to 17 msec/item; \(F(2,14) = 3.44, p = .07\); see Figure 1A]. This differential effect indicates that contour completion, per se, interferes only little with target search. By contrast, a robust interference resulted from distracters that gave rise to (competing) surface information.

A follow-up experiment indicated that the slope increases for form-type distracters did not simply result from physical similarities between inducers that define targets and distracters. In this experiment, eight observers (1 man, mean age 27.3 years) searched for a target configuration that did not comprise an illusory figure (see Figure 1C for an example target [T] configuration). The target had to be detected among varying numbers of distracters, \(F(2,14) = 22.05, p < .001\). Search performance was strongly affected as the number of shared inducers between target and distracter configurations increased (Figure 1C, I–III), even though the target comprised a configuration that did not give rise to the emergence of an illusory figure.
However, clear performance differences were revealed when search performance was compared between target configurations that did and those that did not give rise to an illusory figure, while controlling for the number of inducers shared between the target and distracter configurations. When the target did not comprise an illusory figure (Figure 1C-III), the search rate was markedly decreased, by a factor of four, compared to when the target induced perception of an illusory figure, \( t(14) = 4.61; p < .001, \) two-tailed test (Figure 1B-II). This difference implies that figural grouping processes are exploited in search for a Kanizsa figure and improve performance considerably.

Thus, as an interim conclusion, processes of figure formation that support the filling-in of surface information can have a major impact on visual search performance, interfering with successful target detection (cf. Duncan & Humphreys, 1989). This suggests that search performance might reflect surface filling-in computed by mechanisms within the LOC and the fusiform gyrus (Stanley & Rubin, 2003; Hirsch et al., 1995) rather than supporting a link to illusory contour completion attributed to area V2 (von der Heydt et al., 1984).

The present study was designed to examine the interfering effect of shape information in distracters upon target detection, by investigating variations in the event-related potential (ERP) extracted from the human electroencephalogram (EEG). As elaborated above, visual search performance is subject to specific interference effects of distracter form information on the detection of a target Kanizsa figure (Conci et al., submitted). Given this, the present study was aimed at determining the physiological correlates of form distracter interference. Previous work has typically examined how contour and surface information correlate with a specific neural pattern (e.g., Murray, Wylie, et al., 2002). The present study, by contrast, examined interference from contour and surface. This was done by presenting observers with search displays that contained two candidate target configurations (see Figure 2B for an example display), thereby permitting the impact of a specific distracter attribute (i.e., its border or form) upon detection of the target configuration to be determined. As will be seen, variations in search performance resulting from distracter interference were associated with specific variations within the N2pc component, which is interpreted as reflecting the allocation of attentional resources to a selected target (Eimer, 1996; Luck & Hillyard, 1994a).

METHODS
Participants
Ten right-handed observers (4 men; mean age 26.2 years) with normal visual acuity participated in the experiment for a payment of €8.00 per hour. All observers provided written informed consent, and the experimental procedures were approved by the ethics committee of the Department of Psychology, Division of General and Experimental Psychology, University of Munich.

Apparatus and Stimuli
Stimulus generation, event timing, and trigger signals were controlled by an IBM PC compatible computer. Stimuli were presented in white (1.83 cd/m²) against a black (0.02 cd/m²) background at the bottom left and right quadrants of a 19-in. computer monitor (see Rubin, Nakayama, & Shapley, 1996). Each stimulus configuration was diagonally offset by 8.75° of visual angle from a

Figure 2. (A) Possible pairs of target (T) and distracter (D) configurations in the experiment. The target configuration was always defined as a Kanizsa square. By contrast, distracters were arranged such that three possible configurations resulted, which are referred to as “standard” (I), “border” (II), and “form” (III) types. (B) Example of a target-present search display depicting the two possible stimulus locations in the experiment (see Methods).
central presentation of fixation cross (see Figure 2B for an example). At a viewing distance of 110 cm, each candidate grouping (composed of four inducing elements with a diameter of 1°) subtended a viewing angle of 2.9° × 2.9°. As depicted in Figure 2A, the target (T) was always defined as a Kanizsa square. Distractor (D) configurations were constructed by rotating inducer elements such that these could be categorized as standard (Figure 2A-I), border (Figure 2A-II), or form (Figure 2A-III) types. For the standard distractor, inducers were rotated with the aperture of each inducer facing outwards, so that no illusory figure was induced. By contrast, inducers that supported border and form distracters were arranged such that they promoted emergent contours and, respectively, emergent contours plus surface produced by two “continuations” between neighboring inducer elements. Both border and form distracter types were presented such that the continuations between inducers were oriented at random towards the left, right, bottom, or top.

Procedure

Each trial started with the presentation of a fixation cross for a randomized period of 500–600 msec at the center of the screen. After this period, the two candidate target configurations were presented at the bottom left and right quadrants of the display. Following stimulus onset, observers were to maintain central fixation and respond with a speeded target-absent versus target-present response via mouse keys. Displays remained on screen until a response was given. In case of an erroneous response or a time-out (after 2500 msec), feedback was provided by a computer-generated tone and an alerting message was presented for 500 msec at the center of the screen. Each trial was followed by an interstimulus interval of 1000 msec.

The experiment started with 50 practice trials. Subsequently, 1200 experimental trials were presented in two sessions with six blocks of 100 trials each. For each observer, the response mapping (i.e., left- and right-hand responses to target presence) was pseudorandomly switched from the first to the second session in order to control for compatibility effect between stimulus position and response hand (Fitts & Seeger, 1953). Within each session, the type of distractor was kept constant throughout a block of trials, and distracter blocks were presented in pseudorandom order on an observer-by-observer basis. In summary, the independent variables were target (present, absent), distracter type (standard, border, form), target position (left, right), and response mapping (left, right), with 50 trials per condition.

EEG Recording

The EEG was recorded continuously by a BrainAmps system (Brain Products, München, Germany) from 64 Ag–AgCl electrodes according to the extended 10-10 system with a sampling rate of 500 Hz. The electrodes were mounted in an elastic cap (FM Services, Herrsching, Germany). Vertical and horizontal eye movements were monitored with electrodes placed at the outer canthi of the eyes and the superior and inferior orbits. Electrophysiological signals were amplified and filtered online using a 0.1–100 Hz band pass. All electrodes were referenced to Cz. Signals were then 30-Hz low-pass filtered and averaged offline over a 1000-msec epoch relative to a 200-msec prestimulus baseline. Trials with incorrect responses, excessive peak deflections (i.e., >100 μV), or bursts of electromyographic activity were excluded from averaging. In addition, ocular artifacts (blinks and eye movements) within critical pre- and post-stimulus epochs were corrected by using the Gratton–Coles algorithm (Gratton, Coles, & Donchin, 1983).

RESULTS

Analyses

The experiment was designed to identify physiological correlates of similarity-based interference between attributes of the distracter configuration and attributes of the target figure. Consequently, only target-present trials were included in the initial analysis of behavioral performance and ERPs.

For the behavioral analysis, RTs on trials on which a response error (6.8% target misses) was made were removed from the RT data set prior to analysis. RTs and arcsine-transformed error rates were each analyzed by means of a repeated measures ANOVA with the factors Distracter Type (dt: standard, border, form), Target Position (tp: left, right), and Response Mapping (rm: left, right response button for target presence).

Analysis of the ERPs proceeded from identifying latency windows for the standard P1, N1, and N2 components in the grand-average waveforms. Components were determined in the following poststimulus time windows: 60–120 msec (P1), 120–210 msec (N1), and 210–340 msec (N2). Figure 4 (bottom left) illustrates the corresponding ranges. Within these predefined windows, peak amplitudes and latencies were extracted for the P1, N1, and N2 components. In order to statistically compare amplitudes and latencies for component peaks, repeated measures ANOVAs, with the factors Electrode (electrode 1, electrode 2), Target Position (tp: left, right), and Distracter Type (dt: standard, border, form), were performed separately for selected pairs of posterior electrodes covering striate and extrastriate areas of the visual system (occipital: O1, O2; occipitoparietal: PO7, PO8; parietal: P5, P6).

In a second step of the EEG analysis, the N2pc component was extracted to examine condition-specific variations in further detail by means of lateralized potentials. The N2pc was quantified as the average of the
ipsilateral potential (left electrode with left targets and right electrode with right targets) subtracted from the contralateral potential (left electrode with right targets and vice versa), with data collapsed across left and right target locations. Peak amplitudes and latencies extracted in the 240- to 340-msec range were subjected to analysis. As for the ERPs, a set of posterior electrode pairs (O1, O2; PO7, PO8; P5, P6) was statistically evaluated. For each lateralized component (occipital, occipitoparietal, and parietal), a repeated measures ANOVA was computed with the factor Distracter Type (dt: standard, border, form).

In the final step, the target-absent ERPs were analyzed. Peak amplitudes and latencies were extracted in the N2 range (240–340 msec) in order to examine whether effects revealed in the above EEG analyses are specific to target presence or whether they would also be manifest on target-absent trials. N2-specific peak amplitudes and latencies were evaluated by repeated measures ANOVAs for posterior electrode pairs (O1, O2; PO7, PO8; P5, P6), each with the factors Electrode (electrode 1, electrode 2) and Distracter Type (dt: standard, border, form).

Behavioral Effects

Visual inspection of the RT distribution revealed no pronounced positive skew, which would require the application of correction procedures. Figure 3 presents the mean correct RTs and the error rates as a function of the distracter type for target-present trials.

The RT ANOVA revealed main effects of distracter type (dt) and response mapping (rm): dt, F(2,18) = 4.35, p < .03; rm, F(1,9) = 8.98, p < .02. Response latencies increased from standard through border to form distracters that were presented together with the target. In addition, right-hand responses to target presence were overall faster than left-hand responses. No other significant effects were obtained.

ERP Effects

Figure 4 presents grand-average ERP waveforms elicited at occipital (O), occipitoparietal (PO), and parietal (P) posterior electrodes. Each panel presents the response elicited contralateral to a target Kanizsa square or contralateral to a distracter, presented in the lower left and right quadrants of the visual field, respectively. All waveforms were obtained by averaging corresponding conditions at left (P5, PO7, O1) and right (P6, PO8, O2) electrodes.

Statistical analyses failed to reveal any significant effects in terms of peak latencies and amplitudes for the P1 and N1 components. By contrast, the ANOVAs of the N2 components revealed significant effects in terms of differential peak amplitudes. For occipital electrodes, the main effect of target position (tp), F(1,9) = 8.69, p < .02, and the interactions of electrode with target position (electrode × tp), F(1,9) = 8.53, p < .02, and electrode with distracter type (electrode × dt), F(2,18) = 4.15, p < .04, were significant. The main effect of target position was due to a more negatively inclined deflection for target presentation in the right, as compared to left, hemifield. The interaction of target position with electrode reflected a more negative amplitude deflection for left visual field targets at right hemisphere electrodes and vice versa. Finally, the interaction distracter type with electrode was due to border and form distracters producing a greater negativity than the standard distracter at electrode O1. By contrast, electrode O2 displayed comparable amplitudes for border and standard distracters, and a more negative amplitude only for the form distracter.

Consistent with the significant effect at occipital sites, an interaction between electrode and target position (electrode × tp) was also manifest at occipitoparietal, F(1,9) = 7.08, p < .03, and parietal electrodes, F(1,9) = 8.65, p < .02, in the N2 range. As for occipital electrodes, the interactions were due to larger negative deflections for contralateral target presentations. Maximal variations of this effect were observed for occipitoparietal electrodes. No other significant ERP effects were obtained.

Lateralized Components

Figure 5 presents grand-average difference waves (contra-minus ipsilateral), separately for each distracter type (standard, border, and form distracters). Statistical analyses of the N2pc revealed a significant main effect of distracter type on peak amplitude differences at occipital,
F(2,18) = 4.86, p < .03, occipitoparietal, F(2,18) = 5.88, p < .02, and parietal, F(2,18) = 5.32, p < .02, electrodes. For all three electrode sites, peak amplitude differences between lateralized components were less negative for form distracters than for border and standard distracters.

**Target-absent ERPs**

In contrast to the target-present analyses, statistical evaluation of target-absent peak amplitudes and latencies failed to reveal any significant effects. Thus, the target-absent ERPs show no evidence of either a hemispheric lateralization or variations of the N2 component as a function of distracter type.

**Summary of Results**

Behavioral analysis revealed that the efficiency of visual search for an illusory target figure depends critically upon the specification of distracter attributes. Response latencies and error rates increased from standard through border to form distracters, suggesting that figural information interferes with successful target detection. Presenting illusory contours of the border distracter type concurrently with a target resulted in increased response latencies and error rates. Furthermore, presenting surface information of the form distracter type led to even larger impairments in performance measures. Taken together, the behavioral results strongly suggest that emergent figural information is coded for search, producing stronger interference with target detection for more similar figural information in distracters (consistent with Conci et al., submitted).

Analyses of the ERP data revealed no effects for the early P1 and N1 components. It should be noted, however, that the absence of significant differences in these components does not entirely exclude the possibility that transient activations sensitive to attributes of target and distracters were eliminated by the low-pass filter set at 30 Hz.
Within the N2 time window, significant effects were obtained that reflected more negative deflections contralateral to the stimulated target quadrant. In addition, at left occipital electrodes, the significant interaction of electrode with distracter type revealed that figural information in border and form distracters is processed differently relative to the standard distracter type. In a subsequent step, a narrower time window was chosen for further analysis of lateralized potentials, which revealed specific effects of distracter type. Difference waves exhibited smaller amplitude deflections for form distracters as compared to standard and border distracter types (see Figure 5, black arrow). This is consistent with the pattern of behavioral results and reveals an electrophysiological correspondence of the form distracter interference with detection (or attentional selection) of the target Kanizsa figure. Finally, analogous ERP analyses of the target-absent N2 component failed to reveal corresponding (significant) effects, suggesting that the observed N2 variations with distracter type are specific to the presence of a target in a given display.

This pattern of results supports an account of similarity-based target–distracter interference. On this account, form distracters share most attributes with the target. As a result, the negative deflection contralateral to the form distracter exhibits the highest negativity (see black arrow in Figure 4, PO, right), comparable to activations in response to a target (see black arrow in Figure 4, PO, left), which is why the corresponding lateralized difference curve displays a significantly smaller deflection (see black arrow in Figure 5, electrodes PO8/PO7).

In sum, both behavioral and EEG measures exhibit a pattern of results consistent with an account of similarity-based interference in processing the illusory figure. In particular, presenting emergent form information in distracters interfered most strongly with detection of the target. In correspondence with behavioral performance, the N2pc component displayed the largest negativity when coding form information in distracters, which implies a role in coding (emergent) figural information for target selection.

**DISCUSSION**

The present study was designed to isolate an electrophysiological correlate of similarity-based object interactions in a task involving the detection of a target Kanizsa figure. Although the behavioral results replicated previous work demonstrating that interference results primarily from emergent form information (Conci et al., submitted), analysis of ERPs in the present experiment suggests that this effect can be attributed specifically to the time window from 240 to 340 msec poststimulus at posterior electrode positions. Target selection was reflected in ERP measures in terms of a large N2pc activation for all distracter conditions. By contrast, N2pc activations elicited by distracters depended on...
whether the distracter configuration contained salient attributes shared with the target in the opposite quadrant. Distracters of the standard and border types elicited only relatively small negative deflections, mirroring the efficiency of search performance. By contrast, form distracters yielded a large negative-going deflection that was comparable in magnitude to the target-related activation, and which produced the greatest interference with target detection. Thus, the ERP results mirror behavioral performance and they imply that target selection is influenced or guided by processes that reflect the registration of figurally integrated object (i.e., form) attributes.

In comparison with previous electrophysiological studies that reported activations in response to illusory figures in the N1 component (Murray, Foxe, et al., 2004; Murray, Wylie, et al., 2002; Pegna et al., 2002), the effects revealed in the present study occur relatively late. However, previous experiments presented the illusory figure in isolation rather than requiring the selection of a target among distracters. Thus, the N2pc activation revealed in the present experiment does not necessarily contradict previous work, but rather specifies processes related to the allocation of attention to the position of a predefined target. Consistent with this interpretation is the analysis of ERPs on target-absent trials, which did not reveal any such N2 variations. Thus, the N2 component depends upon the target (see also Luck & Hillyard, 1994b), whereas effects in the N1 component may be attributed to the specification of processes related to stimulus encoding itself (Murray, Wylie, et al., 2002).

The finding of an N2pc-specific effect reflecting the efficiency of allocating attention to the target position is also in close agreement with a variety of experimental reports. Luck and Hillyard (1994a) have shown that an N2pc was elicited by “pop-out” targets defined within a single feature dimension, although being absent in response to all distracters of the stimulus array. Consequently, the N2pc activity may reflect a shift of attention to a relevant target location. Although a variety of stimulus dimensions (such as form or color) gives rise to an N2pc component, the effect can also be observed when the target is presented with just one distracting stimulus (Eimer, 1996). In addition, the N2pc has been reported not only for targets, but also for nontargets that either comprise a salient pop-out feature (Luck & Hillyard, 1994a) or require careful scrutiny to be distinguished from the target (Luck & Hillyard, 1994b). Furthermore, magnetic field recordings suggest that the N2pc mirrors detection of task-relevant features prior to the allocation of spatial attention (Hopf, Boelmans, Schoenfeld, Luck, & Heinze, 2004). Source localization of N2pc-related activity revealed an early parietal component and a later occipital activation pattern (Hopf, Luck, et al., 2000).

Comparing the present findings with previous work reveals close links and correspondences. In agreement with Luck and Hillyard (1994a) and Eimer (1996), the N2pc elicited by a target Kanizsa figure was larger than the corresponding activation elicited by distracter configurations. In addition, similarity between target and distracter configurations was reflected in the lateralized amplitude differences within the occipitoparietal cortex, comparable to the pattern obtained for other reported variations of target discriminability (Luck & Hillyard, 1994b). Whereas large form-based distracter interference was reflected by small amplitude differences, the opposite was observed for (standard and border type) distracters that induced relatively little interference, allowing efficient target detection. The maximum variability of this pattern at occipitoparietal electrodes closely resembles other reports that have investigated the emergence of surface characteristics in area LOC (Stanley & Rubin, 2003; Murray, Wylie, et al., 2002). Consequently, this may be taken to indicate that search performance reflects analysis of candidate target stimuli based upon the completed representation of illusory shape information. Latency ranges (240–340 msec post-stimulus onset) and the occipitoparietal maximum, in addition, roughly correspond to the late occipital magnetic subcomponent extracted within the N2pc time window (Hopf, Luck, et al., 2000).

In conclusion, the observed N2pc modulation may indicate a shift of attention to a relevant target location on the basis of salient region computations (Stanley & Rubin, 2003). Within this framework, computation of surface characteristics, rather than contour interpolations, contribute to salient region estimations that are extracted for a crude initial analysis of the visual scene to guide efficient selection.

Acknowledgments
We thank Shanshan Chen for help in running the experiment, and George R. Mangun and two anonymous reviewers for valuable comments on an earlier version of this manuscript. This work was supported by German Research Foundation (DFG) project Grant EL 248/2 awarded to M. A. E. and H. J. M.

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